# JOURNAL OF THEORETICAL BIOLOGY

*Co-Chief Editors:* S. A. KAUFFMAN
L. WOLPERT

*Editorial Board:* N. BARTON
J. BONNER
A. CORNISH-BOWDEN
J. COWAN
J. A. DANI
F. DYSON
J. M. GELFAND
M. E. GILPIN
L. GLASS
A. GOLDBETER
B. GOODWIN
M. HASSALL
P. W. HEDRICK
T. B. L. KIRKWOOD
J. H. LEWIS
W. R. LIEB
R. B. LUFTIG
R. M. MAY
J. MAYNARD SMITH
J. D. MURRAY
T. OHTA
H. H. PATTEE
A. S. PERELSON
S. L. PIMM
J. RINZEL
M. R. ROSE
M. SAVAGEAU
P. SCHUSTER
T. TAKENAKA
J. TYSON
J. Z. YOUNG

VOLUME 150
*May–June* 1991

ACADEMIC PRESS
London San Diego New York Boston
Sydney Tokyo Toronto

Per.
QH
301
J75

Copyright © 1991, by Academic Press Limited

ALL RIGHTS RESERVED

No part of this volume may be reproduced in any form, by photostat, microfilm, or any other means, without written permission from the publishers.

*Printed in Great Britain*

# Contents for Volume 150

*Number 1, 7 May 1991*

KOHN, M. C., Dedication . . . . . 1

KOHN, M. C. and LEMIEUX, D. R., Identification of Regulatory Properties of Metabolic Networks by Graph Theoretical Modeling . . . . 3

ZHU, C., A Thermodynamic and Biomechanical Theory of Cell Adhesion Part I: General Formulism . . . . . 27

BING-ZHENG, L. and GOU-MIN, D., An Improved Mathematical Model of Hormone Secretion in the Hypothalamo-Pituitary-Gonadal Axis in Man . . . . . 51

QUON, M. J. and CAMPFIELD, L. A., A Mathematical Model and Computer Simulation Study of Insulin Receptor Regulation . . . . . 59

LEMIEUX, D. R. and KOOTSEY, J. M., Simulation of the Voltage Dependence of the Na, K Pump Applied to Cardiac Cells . . . . . 73

QUON, M. J. and CAMPFIELD, L. A., A Mathematical Model and Computer Simulation Study of Insulin Sensitive Glucose Transporter Regulation 93

ACHS, M. J., GARFINKEL, L. and GARFINKEL, D., A Computer Model of Pancreatic Islet Glycolysis . . . . . 109

*Number 2, 21 May 1991*

WALTER, G. H., What is Resource Partitioning? . . . . . 137

FRANCE, J., SIDDONS, R. C., DHANOA, M. S. and THORNLEY, J. H. M., A Unifying Mathematical Analysis of Methods to Estimate Rumen Volume Using Digesta Markers and Intrauminal Sampling . . . . 145

DEXTER, F., RUDY, Y., LEVY, M. N. and BRUCE, E. N., Mathematical Model of Cellular Basis for the Respiratory Sinus Arrhythmia . . . 157

LOEFFLER, M. and GROSSMANN, B., A Stochastic Branching Model with Formation of Subunits Applied to the Growth of Intestinal Crypts . 175

TAWADA, K. and SEKIMOTO, K., Protein Friction Exerted by Motor Enzymes Through a Weak-binding Interaction . . . . . 193

WHITE, R. A., A Theory for Analysis of Cell Populations with Non-cycling S Phase Cells . . . . . 201

AOKI, I., Entropy Principle for Human Development, Growth and Aging 215

VERTOSICK, F. T. and KELLY, R. H., The Immune System as a Neural Network: A Multi-epitope Approach . . . . . 225

RADDING, W., Proposed Partial $\beta$-structures for Lac Permease and the $Na^+/H^+$ Antiporter which use Similar Transport and $H^+$ Coupling Mechanisms 239

ATKINSON, D., Sexual Showiness and Parasite Load: Correlations Without Parasite Coevolutionary Cycles . . . . . 251

LE GUYADER, H. and HYVER, C., Duplication of Cortical Units on the Cortex of Paramecium: A Model Involving a $Ca^{2+}$ Wave . . . . . 261

*Number 3, 7 June 1991*

SANYAL, N. K., OJHA, R. P. and ROYCHOUDHURY, M., Interaction Energy Studies on Antibiotics Nucleoside Analogs 2-Azaadenine . . . 277

TOURTELLOT, M. K., COLLINS, R. D. and BELL, W. J., The Problem of Movelength and Turn Definition in Analysis of Orientation Data . 287

FORBES, L. S., Optimal Size and Number of Offspring in a Variable Environment . . . . . 299

DAVIS, D. N., Models for the Movement of Mono-oriented Chromosomes 305

MATTHECK, C. and REUSS, S., The Claw of the Tiger: An Assessment of its Mechanical Shape Optimization . . . . . 323

VICKERS, G. T., Spatial Patterns and Travelling Waves in Population Genetics 329

NOWAK, M., The Evolution of Viruses. Competition Between Horizontal and Vertical Transmission of Mobile Genes . . . . . 339

ALEXANDER, R. McN., Optimum Timing of Muscle Activation for Simple Models of Throwing . . . . . 349

HAIG, D., Developmental Asynchrony and Environmental Sex Determination in Alligators . . . . . 373

PENOTTI, F. E., Human Pre-mRNA Splicing Signals . . . . . 385

*Number 4, 21 June 1991*

LIBERMAN, U., On the Relation Between the Instability of ESS in Discrete Dynamics and Segregation Distortion . . . . . 421

WANG, Z.-X., Theoretical Considerations of the Tsou Plot . . . . 437

FORSDYKE, D. R., Early Evolution of MHC Polymorphism . . . 451

SMITH, B. R., WOJTOWICZ, J. M. and ATWOOD, H. L., Maximum Likelihood Estimation of Non-uniform Transmitter Release Probabilities at the Crayfish Neuromuscular Junction . . . . . 457

WARBURTON, K. and LAZARUS, J., Tendency-Distance Models of Social Cohesion in Animal Groups . . . . . 473

GLASS, J. D., A Sequence Related to the Human Gonadoliberin Precursor Near the N-termini of HIV and SIV *gag* Polyproteins . . . . 489

MCKNIGHT, K. B and ROUNDY, R. O., Optimal Gill Packing in Agaric Sporocarps . . . . . 497

COHEN, R. J., Determining Rate Constants for Irreversible Polymerization Where the Initial Step and Propagation Steps Have Different Rate Constants: Consideration of Polyadenylate Polymerase . . . . 529

QUINN, T. P., Models of Pacific Salmon Orientation and Navigation on the Open Ocean . . . . . 539

KIANI, M. F. and HUDETZ, A. G., Computer Simulation of Growth of Anastomosing Microvascular Networks . . . . . 547

LETTER TO THE EDITOR

HURST, L. D. and NURSE, P., A Note on the Evolution of Meiosis . 561

## Index to Volume 150

ACHS, M. J., GARFINKEL, L. and GARFINKEL, D., A computer model of pancreatic islet glycolysis, 109
Adhesion, cell; general formulism of a thermodynamic and biomechanical theory, 27
Agaric sporocarps, optimal gill packing in, 497
Aging, human, entropy principle for, 215
ALEXANDER, R. McN., Optimum timing of muscle activation for simple models of throwing, 349
Alligators, developmental asynchrony and environmental sex determination in, 373
Anastomosing microvascular networks, computer simulation of growth of, 547
Animal groups, tendency-distance models of social cohesion in, 473
Antibiotics nucleoside analogs 2-azaadenine, interaction energy studies on, 277
Antiporter, $Na^+/H^+$, proposed partial $\beta$-structures for lac permease and; use of similar transport and $H^+$ coupling mechanisms, 239
AOKI, I., Entropy principle for human development, growth and aging, 215
Arrhythmia, sinus, respiratory, mathematical model of cellular basis for, 157
Asynchrony, developmental, and environmental sex determination in alligators, 373
ATKINSON, D., Sexyal showiness and parasite load: correlations without parasite coevolutionary cycles, 251
ATWOOD, H. L. (see SMITH, B. R.), 457
2-Azaadenine: interaction studies on antibiotics nucleoside analogs, 277

BELL, W. J. (see TOURTELLOT, M. K.), 287
$\beta$-structures, partial, proposed, for lac permease and the $Na^+/H^+$ antiporter which use similar transport and $H^+$ coupling mechanisms, 239
BING-ZHENG, L. and GOU-MIN, D., An improved mathematical model of hormone secretion in the hypothalamo-pituitary-gonadal axis in man, 51
Biomechanical and thermodynamic theory of cell adhesion; general formulation, 27
BRUCE, E. N. (see DEXTER, F.), 157

$Ca^{2+}$ wave in a model of duplication of cortical units on the cortex of paramecium, 261
CAMPFIELD, L. A. (see QUON, M. J.), 59, 93
Cardiac cells, simulation of the voltage dependence of the Na, K pump applied to, 73
Cell adhesion: general formulism of a thermodynamic and biomechanical theory, 27
Cells, cardiac, simulation of the voltage dependence of the Na, K pump applied to, 73
Cell populations with non-cycling S phase cells, a theory for analysis of, 201
Cellular basis for the respiratory sinus arrhythmia, mathematical model of, 157
Chromosomes, mono-oriented, models for the movement of, 305
Claw of the tiger: an assessment of its mechanical shape optimization, 323
Coevolutionary cycles, parasite, correlations without; sexual showiness and parasite load, 251
COHEN, R. J., Determining rate constants for irreversible polymerization where the initial step and propagation steps have different rate constants: consideration of polyadenylate polymerase, 529
Cohesion, social, in animal groups, tendency-distance sensitive models of, 473
COLLINS, R. D. (see TOURTELLOT, M. K.), 287
Competition between horizontal and vertical transmission of mobile genes; the evolution of viruses, 339
Computer model of pancreatic islet glycolysis, 109

Computer simulation of growth of anastomosing microvascular networks, 547
Computer simulation of insulin receptor regulation, 59
Computer simulation study of insulin sensitive glucose transporter regulation, 93
Cortical unit duplication on the cortex of paramecium: a model involving a $Ca^{2+}$ wave, 261
Crayfish neuromuscular junction, maximum likelihood estimation of non-uniform transmitter release probabilities at, 457
Crypts, intestinal, a stochastic branching model with formation of subunits applied to the growth of, 175

DAVIS, D. N., Models for the movement of mono-oriented chromosomes, 305
Dedication, 1
Development, human, entropy principle for, 215
Developmental asynchrony and environmental sex determination in alligators, 373
DEXTER, F., RUDY, Y., LEVY, M. N. and BRUCE, E. N., Mathematical model of cellular basis for the respiratory sinus arrhythmia, 157
DHANOA, M. S. (see FRANCE, J.), 145
Digesta markers, a unifying mathematical analysis of methods to estimate rumen volume using, 145
Dynamics, discrete, and segregation distortion, on the relation between the instability of ESS in, 421

Entropy principle for human development, growth and aging, 215
Environment, variable, optimal size and number of offspring in, 299
Environmental sex determination in alligators, developmental asynchrony and, 373
Enzymes, motor, protein friction exerted by, through a weak-binding interaction, 193
ESS instability in discrete dynamics and segregation distortion, on the relation between, 421
Evolution, early, of MHC polymorphism, 451
Evolution of meiosis, a note on (letter), 561
Evolution of viruses. Competition between horizontal and vertical transmission of mobile genes, 339

FORBES, L. S., Optimal size and number of offspring in a variable environment, 299
FORSDYKE, D. R., Early evolution of MHC polymorphism, 451
FRANCE, J., SIDDONS, R. C., DHANOA, M. S. and THORNLEY, J. H. M., A unifying mathematical analysis of methods to estimate rumen volume using digesta markers and intrauminal sampling, 145
Friction, protein, exerted by motor enzymes through a weak-binding interaction, 193

*gag* polyproteins, HIV and SIV, a sequence related to the human gonadoliberin precursor near the N-termini of, 489
GARFINKEL, D. (see ACHS, M. J.), 109
GARFINKEL, L. (see ACHS, M. J.), 109
Genes, mobile, competition between horizontal and vertical transmission of; the evolution of viruses, 339
Genetics, population, spatial patterns and travelling waves in, 329
Gill packing, optimal, in agaric sporocarps, 497
GLASS, J. D., A sequence related to the human gonadoliberin precursor near the N-termini of HIV and SIV *gag* polyproteins, 489
Glucose transporter regulation, insulin sensitive, a mathematical model and computer simulation study of, 93
Glycolysis, pancreatic islet, a computer model of, 109
Gonadal-hypothalamo-pituitary axis in man, an improved mathematical model of hormone secretion in, 51

Gonadoliberin precursor, human; a related sequence near the N-termini of HIV and SIV *gag* polyproteins, 489
GOU-MIN, D. (see BING-ZHENG, L.), 51
Graph theoretical modeling, identification of regulatory properties of metabolic networks by, 3
GROSSMANN, B. (see LOEFFLER, M.), 175
Groups, animal, tendency-distance models of social cohesion in, 473
Growth of anastomosing microvascular networks, computer simulation of, 547
Growth, human, entropy principle for, 215
Growth of intestinal crypts, a stochastic branching model with formation of subunits applied to, 175

HAIG, D., Developmental asynchrony and environmental sex determination in alligators, 373
HIV and SIV *gag* polyproteins, a sequence related to the human gonadoliberin precursor near the N-termini of, 489
Hormone secretion in the hypothalamo-pituitary-gonadal axis in man; an improved mathematical model, 51
HUDETZ, A. G. (see KIANI. M. F.), 547
Human development, growth and aging, entropy principle for, 215
Human gonadoliverin precursor; a related sequence near the N-termini of HIV and SIV *gag* polyproteins, 489
Human pre-mRNA splicing signals, 385
HURST, L. D. and NURSE, P., A note on the evolution of meiosis (letter), 561
$H^+$ coupling mechanisms; proposed partial $\beta$-structures for lac permease and the $Na^+/H^+$ antiporter, 239
Hypothalamo-pituitary-gonadal axis in man, an improved mathematical model of hormone secretion in, 51
HYVER, C. (see LE GUYADER, H.), 261

Immune system as a neural network: a multi-epitope approach, 225
Instability of ESS in discrete dynamics and segregation distortion, on the relation between, 421
Insulin receptor regulation, a mathematical model and computer simulation study of, 59
Insulin sensitive glucose transporter regulation, a mathematical model and computer simulation study of, 93
Interaction energy studies on antibiotics nucleoside analogs 2-azaadenine, 277
Intestinal crypts, a stochastic branching model with formation of subunits applied to the growth of, 175
Intrauminal sampling, a unifying mathematical analysis of methods to estimate rumen volume using digesta markers and, 145

KELLY, R. H. (see VERTOSICK, F. T.), 225
KIANI, M. F. and HUDETZ, A. G., Computer simulation of growth of anastomosing microvascular networks, 547
KOHN, M. C., Dedication, 1
KOHN, M. C. and LEMIEUX, D. R., Identification of regulatory properties of metabolic networks by graph theoretical modeling, 3
KOOTSEY, J. M. (see LEMIEUX, D. R.), 73

Lac permease and the $Na^+/H^+$ antiporter, proposed partial $\beta$-structures for; use of similar transport and $H^+$ coupling mechanisms, 239
LAZARUS, J. (see WARBURTON, K.), 473
LE GUYADER, H. and HYVER, C., Duplication of cortical units on the cortex of paramacium: a model involving a $Ca^{2+}$ wave, 261

LEMIEUX, D. R. and KOOTSEY, J. M., Simulation of the voltage dependence of the Na, K pump applied to cardiac cells, 73
LEMIEUX, D. R. (see KOHN, M. C.), 3
LEVY, M. N. (see DEXTER, F.), 157
LIBERMAN, U., On the relation between the instability of ESS in discrete dynamics and segregation distortion, 421
LOEFFLER, M. and GROSSMANN, B., A stochastic branching model with formation of subunits applied to the growth of intestinal crypts, 175

MCKNIGHT, K. B. and ROUNDY, R. O., Optimal gill packing in agaric sporocarps, 497
MATTHECK, C. and REUSS, S., The claw of the tiger: an assessment of its mechanical shape optimization, 323
Mechanical shape optimization; claw of the tiger, 323
Meiosis, a note on the evolution of (letter), 561
Metabolic networks: identification of regulatory properties by graph theoretical modeling, 3
MHC polymorphism, early evolution of, 451
Microvascular networks, anastomosing, computer simulation of growth of, 547
Motor enzymes, protein friction exerted by, through a weak-binding interaction, 193
Movelength and turn definition in analysis of orientation data, the problem of, 287
Movement of mono-oriented chromosomes, models for, 305
Muscle activation: optimal timing for simple models of throwing, 349

Navigation of Pacific salmon on the open ocean, models of, 539
Networks, metabolic; identification of regulatory properties by graph theoretical modeling, 3
Networks, microvascular, anastomosing, computer simulation of growth of, 547
Network, neural, the immune system as; a multi-epitope approach, 225
Neural network, the immune system as; a multi-epitope approach, 225
Neuromuscular junction, crayfish, maximum likelihood estimation of non-uniform transmitter release probabilities at, 457
NOWAK, M., The evolution of viruses. Competition between horizontal and vertical transmission of mobile genes, 339
N-termini of HIV and SIV *gag* polyproteins, a sequence related to the human gonadoliberin precursor near, 489
NURSE, P. (see HURST, L. D.), 561

Offspring in a variable environment, optimal size and number of, 299
OJHA, R. P. (see SANYAL, N. K.), 277
Orientation data, the problem of movelength and turn definition in analysis of, 287
Orientation and navigation of Pacific salmon on the open ocean, models of, 539

Pacific salmon orientation and navigation on the open ocean, models of, 539
Pancreatic islet glycolysis, a computer model of, 109
Paramecium, duplication of cortical units on the cortex of; a model involving a $Ca^{2+}$ wave, 261
Parasite load and sexual showiness; correlations without coevolutionary cycles, 251
Patterns, spatial, and travelling waves in population genetics, 329
PENOTTI, F. E., Human pre-mRNA splicing signals, 385
Pituitary–hypothalamo–gonadal axis in man, an improved mathematical model of hormone secretion in, 51
Polyadenylate polymerase: determining rate constants for irreversible polymerization, 529
Polymerization, irreversible, determining rate constants for; consideration of polyadenylate polymerase, 529
Polymorphism, MHC, early evolution of, 451

Polyproteins, *gag*, HIV and SIV, a sequence related to the human gonadoliberin precursor near the N-termini of, 389
Populations, cell, with non-cycling S phase cells, a theory for analysis of, 201
Population genetics, spatial patterns and travelling waves in, 329
Pre-mRNA splicing signals, human, 385
Protein friction exerted by motor enzymes through a weak-binding interaction, 193
Pump, Na, K, simulation of the voltage dependence of, applied to cardiac cells, 73

QUINN, T. P., Models of Pacific salmon orientation and navigation on the open ocean, 539
QUON, M. J. and CAMPFIELD, L. A., A mathematical model and computer simulation study of insulin receptor regulation, 59
QUON, M. J. and CAMPFIELD, L. A., A mathematical model and computer simulation study of insulin sensitive glucose transporter regulation, 93

RADDING, W., Proposed partial $\beta$-structures for lac permease and the $Na^+/H^+$ antiporter which use similar transport and $H^+$ coupling mechanisms, 239
Rate constant determination for irreversible polymerization; consideration of polyadenylate polymerase, 529
Receptor, insulin, regulation, a mathematical model and computer simulation study of, 59
Regulation, glucose transporter, insulin sensitive, a mathematical model and computer simulation study of, 93
Regulation, insulin receptor, a mathematical model and computer simulation study of, 59
Regulatory properties of metabolic networks: identification by graph theoretical modeling, 3
Resource partitioning, what is?, 137
Respiratory sinus arrhythmia, mathematical model of cellular basis for, 157
REUSS, S. (see MATTHECK, C.), 323
ROUNDY, R. O. (see MCKNIGHT, K. B.), 497
ROYCHOUDHURY, M. (see SANYAL, N. K.), 277
RUDY, Y. (see DEXTER, F.), 157
Rumen volume, a unifying mathematical analysis of methods for estimation of, using digesta markers and intrauminal sampling, 145

S phase cells, non-cycling, a theory for analysis of cell population with, 201
SANYAL, N. K., OJHA, R. P. and ROYCHOUDHURY, M., Interaction energy studies on antibiotics nucleoside analogs 2-azaadenine, 277
Segregation distortion, on the relation between the instability of ESS in discrete dynamics and, 421
SEKIMOTO, K. (see TAWADA, K.), 193
Sequence related to the human gonadoliberin precursor near the N-termini of HIV and SIV *gag* polyproteins, 489
Sex determination, environmental, in alligators, developmental asynchrony and, 373
Sexual showiness and parasite load: correlations without parasite coevolutionary cycles, 251
Shape optimization; claw of the tiger, 323
Showiness, sexual, and parasite load: correlations without parasite coevolutionary cycles, 251
SIDDONS, R. C. (see FRANCE, J.), 145
Sinus arrhythmia, mathematical model of cellular basis for, 157
SIV *gag* polyproteins, a sequence related to the human gonadoliberin precursor near the N-termini of HIV and, 489
Size, optimal, of offspring in a variable environment, 299
SMITH, B. R., WOJTOWICZ, J. M. and ATWOOD, H. L., Maximum likelihood estimation of non-uniform transmitter release probabilities at the crayfish neuromuscular junction, 457
Social cohesion in animal groups, tendency-distance models of, 473
Na, K pump, simulation of the voltage dependence of, applied to cardiac cells, 73

$Ha^+/H^+$ antiporter, proposed partial $\beta$-structures for lac permease and; use of similar transport and $H^+$ coupling mechanisms, 239
Spatial patterns and travelling waves in population genetics, 329
Splicing signals, pre-mRNA, human, 385
Sporocarps, agaric, optimal gill packing in, 497
Stochastic branching model with formation of subunits applied to the growth of intestinal crypts, 175
Subunits, a stochastic branching model with formation of; application to growth of intestinal crypts, 175

TAWADA, K. and SEKIMOTO, K., Protein friction exerted by motor enzymes through a weak-binding interaction, 193
Tendency-distance models of social cohesion in animal groups, 473
Thermodynamic and biomechanical theory of cell adhesion; general formulism, 27
THORNLEY, J. H. M. (see FRANCE, J.), 145
Throwing, optimum timing of muscle activation for simple models of, 349
Tiger claw: an assessment of its mechanical shape optimization, 323
TOURTELLOT, M. K., COLLINS, R. D. and BELL, W. J., The problem of movelength and turn definition in analysis of orientation data, 287
Transport mechanism; proposed partial $\beta$-structures for lac permease and the $Na^+/H^+$ antiporter, 239
Travelling waves and spatial patterns in population genetics, 329
Tsou plot, theoretical considerations of, 437
Turn definition in analysis of orientation data, the problem of movelength and, 287

VERTOSICK, F. T. and KELLY, R. H., The immune system as a neural network: a multi-epitope approach, 225
VICKERS, G. T., Spatial patterns and travelling waves in population genetics, 329
Virus evolution: competition between horizontal and vertical transmission of mobile genes, 339
Voltage dependence of the Na, K pump applied to cardiac cells, simulation of, 73

WALTER, G. H., What is resource partitioning?, 137
WANG, Z.-X., Theoretical considerations of the Tsou plot, 437
WARBURTON, K. and LAZARUS, J., Tendency-distance models of social cohesion in animal groups, 473
Weak-binding interaction, protein friction exerted by motor enzymes through, 193
WHITE, R. A., A theory for analysis of cell populations with non-cycling S phase cells, 201
WOJTOWICZ, J. M. (see SMITH, B. R.), 457

ZHU, C., A thermodynamic and biomechanical theory of cell adhesion. Part I: general formulism, 27